# THE EXPERIMENTAL DATA OF THE MUTATION THEORY.

## B. EXPERIMENTS WITH OENOTHERA.*

CONVINCED that the origin of specific characters should be amenable to experimental investigations, Professor De Vries began in 1886 a search for suitable material for his researches. He brought more than one hundred species of the native and introduced flora to his garden; his purpose in doing this was not their improvement by selection but simply to secure convenience and accuracy of observation which would have been quite impossible with the plants still in the open. One of the species, however, showed itself quite different from the others, and the history of this form we shall now relate in its main points, as briefly as possible.

In a deserted potato field near Hilversum an American primrose, *Oenothera Lamarckiana*, often cultivated in the European gardens and running wild extensively, had been growing for about ten years as an escape from a neighboring source and had taken possession of about half of the field where it was represented by hundreds of individuals when the spot was noticed in 1885. The plants showed the usual fluctuating variability in a pronounced degree as well as occasional malformations, such as fasciations and the transformation of leaves into conical pitchers, but

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it was not until the next summer that the most important discovery was made.

Then two groups of plants, each of only a few individuals, but of a well characterized and distinct form, were discovered, and it seemed at once evident that these belonged to a new elementary species and that it was not improbable from their limited areas of distribution that they had each sprung from the seed of a single individual. No comparable forms were found in the great herbaria at Leiden, Paris or Kew. More significant still, the forms showed themselves constant in culture from the first. One of the new species was designated as *Oenothera brevistylis* because of the much shorter style, while the other, with smooth leaves and much handsomer foliage than *O. Lamarckiana* and conspicuous for the habit of producing petals which lack the notch at the margin, was called *O. laevifolia.*

The characteristics separating these species from the parent, *O. Lamarckiana,* are many and not merely those given above, but here, as with all other species mentioned in this paper, space cannot be given to detailed descriptions which would hardly be of interest to the general reader. Nor can we attempt to describe in any detail the series of laborious cultural experiments which followed the discovery of the two new elementary species in the deserted potato field at Hilversum. The merest outline must suffice, for it is the object of the present paper with its limited space to present the philosophy of the mutation theory as compared with the theory of fluctuating variations with just enough illustrative examples, rather than to give a detailed review or criticism of the data upon which the theory rests.

In the fall of 1886 two lots of material of *O. Lamarckiana* were selected for the experimental garden at Amsterdam. The first consisted of nine rosettes, and the second

a quantity of seed. Besides these, seed was collected from the newly discovered *O. laevifolia* and plants of *O. brevistylis* were taken bodily. Occasionally seed was taken from the original locality for check tests.

In accordance with the terminology of sugar beet selection the first three groups were designated as families and as such have been cultivated to the present time.

The descendants of the rosettes formed the *Lamarckiana* family, those from the seed of the *O. laevifolia* the *Laevifolia* family, and from the seed of the five-celled *O. Lamarckiana* fruit came a group designated as the *Lata* family. We may confine our attention here to the *Lamarckiana* family.

The rosettes taken from the field at Hilversum flowered in an isolated bed and produced an abundance of seed, from which, as the second generation, about fifteen thousand individuals were produced, among which were found two forms not seen before. These were distinguished as *O. nanella* and *O. lata* and were represented by five individuals each.

Six typical specimens of *Lamarckiana* served as seed plants, and in the third generation of about ten thousand individuals three each of the two new forms mentioned appeared, and in addition *O. rubrinervis*, of which one example was observed.

For the sake of improving methods of cultivation and artificial pollination it was necessary to discontinue the further cultivation of the *Lamarckiana* family for a time, but when it was again resumed four years later, the fourth generation of about fourteen thousand plants was found to contain three hundred and thirty-four of the mutated individuals, of which one-half belonged to four forms which had not yet shown themselves in the cultures, *O. gigas, O. albida, O. oblonga* and *O. scintillans*. The culture was conducted for four generations more with a greater

or lesser number of individuals, and always with a number of the newly originated forms though no more new types appeared in these later generations. In all of these, however, the total number of individuals was less than that of the fourth generation alone. The eight generations numbered about fifty thousand individuals of which about eight hundred were mutants belonging to seven new elementary species. Of these, but one appeared only a single time.

During the first years of the experiment the plants were so isolated that there was no danger of crossing with any other form, but later the flowers were covered with transparent paper bags and self-fertilized so there could be no possibility of hybridity. It is thus certain that the ancestors of each of these eight hundred new forms produced between 1888 and 1899 had had typical *O. Lamarckiana* ancestors as far back as 1886 and in all probability much further.

For the botanical specialist it would be highly desirable to present detailed descriptions of these new species, but it would be of little interest to the general reader, and it must suffice to say that, though the differences are small, they are many and so well defined that there is no danger of mistaking the new forms. Indeed some of them may be at once recognized in the seedling stages, though others require a greater degree of maturity to exhibit their characteristics. It is altogether probable that one and one-half per cent. does not represent the total number of distinctly new forms, since it was necessary to weed out the most of the individuals as soon as they showed distinctive characters, and it is quite probable that some of these examples cast aside as typical *O. Lamarckiana* would have later, perhaps when flowering, shown themselves to be separable from the parent by well defined differences. A brief account of the origin of these new forms and their conduct

under cultivation will be much more profitable than technical descriptions.

*O. gigas* was the only one of the seven forms which was observed but a single time in the *Lamarckiana* family. In the other families it appeared but twice. This single individual which had had for at least three generations typical *O. Lamarckiana* as ancestors, formed the beginning of the new species *O. gigas*. From the seed of this self-fertilized individual there were grown over four hundred and fifty plants. These were conspicuous for their constancy to the new specific type which differed clearly and sharply from *O. Lamarckiana*. Only a single aberrant individual was found. This showed the characteristics of *O. gigas* but was a dwarf and so was given the varietal name of *O. gigas nanella*. Not one reverted to the characteristics of the *O. Lamarckiana*. Thus a new elementary species may originate in a single individual and be perfectly constant from the first.

*O. albida,* occurring every year in greater or lesser numbers in the most of the cultures, is a very characteristic form, at first considered pathological individuals and not counted. Even when it was recognized that this represented a distinct type it was long before the weak plants could be brought to flower and mature fruit. When this was finally accomplished only a few seeds were produced and so the experiment was not an extensive one, but so far as it was carried the form was perfectly constant in the second and third generations.

*O. rubrinervis* is distinguished from the others by its form and the characteristic red coloration of the veins of the leaves and the stripes on the calyx. It also exhibits a high degree of brittleness due to the limited development, though not entire absence, of the strengthening bast portion of the stem. A slight blow or lack of care in the plucking of a fruit is sufficient to break the stem into a

number of pieces. This characteristic never failed; every plant classed in its rosette stage as *rubrinervis* could be counted on to produce later a very brittle stem and red calyx and fruit. In the year 1896 about one thousand examples of this species were grown from seed produced by eight individuals which had originated immediately from the *O. Lamarckiana* stock the year before. All were typical *rubrinervis* except for two plants. One of these had the characteristics of a new species, here appearing for the first time, and was designated as *O. leptocarpa,* while the other was clearly *O. Lamarckiana,* probably from a seed already in the ground. This plant was naturally the cause of some concern, but all doubt was removed when two check experiments, aggregating nearly three thousand plants, showed the species perfectly constant, and justified the conclusion that *O. rubrinervis* is a good elementary species.

*O. oblonga* appeared in every generation after the third and in considerable numbers, being recognizable when the seedlings had produced about the sixth leaf. The seed from seven biennial plants produced 1683 seedlings all of which, excepting one with the characteristics of *O. albida,* were typical *O. oblonga.* The seed of the annual plants germinated poorly, only 64 plants being produced. With the exception of one *O. rubrinervis,* all were true. In neither lot were the *O. Lamarckiana* characteristics to be recognized. *O. oblonga* may then be regarded as constant from its first appearance but with the power of producing other new forms.

In the preceding forms and in those which are to follow there is nothing comparable with the results of general horticultural experience with other plants. In *O. nanella,* the dwarf primrose appearing in every generation, we have a form which is very similar to the dwarf varieties which occur in so many cultivated plants.

But some one will at once suggest that such forms are only varieties and not species. In truth these dwarfs may as well be called *O. Lamarckiana nanella* as *O. nanella.* So long as ambiguity does not result, it is quite unessential whether an organism with a given set of characteristics be spoken of as species or variety. The point of real interest is to know whether these characteristics are heritable and constant or whether they are merely the expression of a widely fluctuating variability to be lost in succeeding generations. Since *O. nanella* differs from the parent form in only the one characteristic—that of size—perhaps it may be as well to speak of it as a variety, but if in cultivation it shows itself true to seed it must be remembered that is as worthy of the name of an elementary species as are other constant forms.

*O. nanella* is probably the most easily recognized of the new forms, unless it be *O. lata,* throughout its entire development, beginning as early as the second leaf. The first counting for this species, or variety, was made with 440 plantlets, from seed of self-fertilized parents. All of these showed themselves true. As a second experiment twenty individuals, originating immediately and without transition from *O. Lamarckiana,* were self-fertilized and produced 2463 seedlings, all of which were the typical dwarf form. A still more extensive experiment was that in which 36 plants were self-fertilized and produced over 18,000 typical *O. nanella* seedlings, among which the only deviations were three plants showing the additional characteristics of *O. oblonga,* which may therefore be designated as an elementary type of second rank, *O. nanella oblonga.* When *O. nanella* occurred in other families it was very constant. Forms in which the characters of more than one species were noted, as *O. lata nanella, O. nanella elliptica,* etc., were very rare.

As soon as the second or third leaf unfolds, the species

known as *O. lata* is recognizable. It appears almost regularly, but in exceedingly variable numbers representing from 0.1 to 1.8 per cent. of the entire culture. In addition to its other characteristics, this form is always purely pistillate, no fertilization with its own scanty pollen ever having succeeded. Crosses with the pollen of *O. Lamarckiana* were almost perfectly fertile and produced in the second generation from 15 to 20 per cent. of *O. lata* plants.

The six new elementary species just described have been characterized by a remarkable degree of constancy, showing in the many thousands of individuals only one plant of *O. Lamarckiana,* and this was without doubt due to a seed in the soil. Only rarely have the new species shown the power of giving rise to other new forms. But in the seventh of the series originating from the main stem of the *Lamarckiana* family during its eight generations, *O. scintillans* shows quite different characteristics. With the exception of *O. gigas* and some others not yet described, *O. scintillans* is the rarest of the new species. With self-fertilization it produces not pure *O. scintillans,* but *O. scintillans, O. oblonga,* and *O. Lamarckiana,* and in a more or less definite numerical proportion. Two groups seem to occur, one with 30 to 40 per cent. and the other with about 70 or more per cent. of the offspring true to the parent type.

We have discussed as briefly as possible the plants belonging to the *Lamarckiana* family. Earlier in this paper we referred to other lots of plants which were brought from the field at Hilversum. Each of these families was followed through, generation by generation, by the experimenter, and his results are described in detail under the headings: A Side Branch of the *Lamarckiana* Family, The *Laevifolia* Family, Two *Lata* Families, Mutation in Other Families, and Mutation in Nature. The results of these

investigations confirm those obtained in the *Lamarckiana* family so that we need not describe them here.

These "families," as De Vries has termed them, represent the principal experiments carried on for the purpose of observing the origin of new forms. Besides these extensive investigations, however, many sowings and countings were made for other purposes. These all furnish confirmatory evidence in support of the conclusions drawn from the more extensive and longer continued experiments. It may almost be said that mutations occurred in every extensive culture.

In general the new species are less mutable than the original *O. Lamarckiana* from which they spring, but there also occur among the new species very strongly mutable forms such as *O. scintillans.*

In crossing, the tendency to mutation is retained, and when *O. Lamarckiana* is produced from crossing it seems to exhibit the tendency in all its strength, Sowings of *O. leptocarpa, O. nanella* and *O. oblonga* proved true to type except for seven individuals in 3410 seedlings counted. The mutants in these cases represent about 0.2 per cent. of the individuals while from the seed of *O. Lamarckiana* from one to three per cent. or more are produced.

*O. scintillans* is a very mutable new species. Only about one-third of the offspring are true to the parent type while the other two-thirds are *O. oblonga* and *O. Lamarckiana* with a few mutants belonging mostly to *O. lata* and *O. nanella.* During six years of cultivation 38 specimens of *O. lata* and 29 of *O. nanella* were found among 7872 seedlings of typical self-fertilized *O. scintillans.* The 67 mutant individuals belonging to the two species represent about 1 per cent. of the total number, a percentage which approaches very closely that yielded by *O. Lamarckiana* itself.

Hybridization seems to increase mutability. The two

parent forms are found in the progeny of these crosses and in case *O. Lamarckiana* is not one of the parents it generally occurs as well. Crosses between *O. Lamarckiana* and *O. nanella* gave during the five years in which the experiment was tried 64 mutant individuals, *O. albida, lata, oblonga, rubrinervis* and *elliptica,* among the 8283 seedlings examined, or about 1 per cent. Among 1586 individuals produced by crossing *O. lata* and *O. nanella* during six years of experimentation, 31 mutated individuals, 15 *O. albida,* 14 *O. oblonga,* and 2 *O. rubrinervis,* were found, or about 2 per cent.

Crossings with the old and accepted species of the systematist, *O. biennis* and *O. suaveolens,* were also tried. *O. Lamarckiana* and the new *O. lata* were crossed with both of these older species and 1352 of the offspring examined. Mutated individuals belonging to the species *oblonga, lata, nanella, elliptica, scintillans* and *albida* occurred to the number of 29, or somewhat more than 2 per cent.

In all of these cases, then, the potency for mutation is about the same as in *O. Lamarckiana* itself.

As we have already mentioned, *O. Lamarckiana* itself often appears among the seedlings from crossed individuals. De Vries has made a comparison of the progeny of this species when produced as the result of crossing, with that of the other new species when produced in the same way, and has arrived at the conclusion that if seed be gathered from plants belonging to one of the new forms, results which correspond with those given above for the production of mutants from new forms are secured, that is to say about 0.2 per cent., while if that from self-fertilized *O. Lamarckiana* be sown the same tendency to mutation will be seen in the richness of the beds in mutated individuals.

In 1889 seedlings were raised from *O. Lamarckiana*

plants grown from crosses between *O. Lamarckiana* and *O. nanella, O. lata* and *O. Lamarckiana, O. lata* and *O. nanella*, and *O. lata* and *O. brevistylis.* In all, 43 mutated individuals, belonging to *O. albida, lata, nanella* and *oblonga,* were found among the 4599 seedlings examined.

About 1 per cent. of mutated individuals in these experiments compares very favorably with the other trials of the mutability of *O. Lamarckiana,* and a general survey of the experiments carried on by Professor De Vries leads us to the conclusion that whatever its source and whatever the number of generations through which it has been cultivated *O. Lamarckiana* retains a very constant potency for mutation. The new species, on the other hand, show their constancy not only by the absence of transition between themselves and reversion to the parent type but by their greatly reduced mutability as well. The capacity for mutation, however, seems to have been transmitted, though in a greatly reduced degree, from the parent to the daughter species, where it is to be seen in the production of an occasional mutant.

The theory of the origin of species by selection has been so long accepted that the term "experimental evolution" conveys at once to the mind a series of experiments in selection or in the modification of organic forms by controlled external forces. To preclude any such misunderstanding of the garden experiments carried on in Amsterdam we must repeat that in the main families described above there was no attempt at selection or the experimental production of mutations, a problem of highest importance for future investigation. The only purpose of the methods employed was to provide a convenient and accurate method of investigating the process which is taking place in nature.

These are two ways of observing mutation as it occurs in nature. The plants may be sought and studied in the

field, or large quantities of seed may be gathered and germinated under conditions favorable for growth and study. The first method is one of exceeding difficulty, and De Vries is the only investigator who has surely succeeded with it even in the most limited degree. The percentage of new forms is so small even when all the seeds are germinated and the number of seeds which reach or at most survive even the seedling stage is so few that this method must be discarded as quite beyond the limits of practicability. With large sowings of seed collected from the plants as they grow in the woods and fields, however, the case is quite different, and we may look with much hope of success to this method. The mutation is already determined in the seed, and germination in the greenhouse or garden affords only the possibility of accurate observation and counting.

Numerous sowings of this kind made by De Vries convinced him that species are for the most part in an immutable condition. It is quite probable, however, that further experiments in different regions will reveal other species which are in the same condition of instability as *O. Lamarckiana*.

Some of the new species of primroses were observed in the original habitat near Hilversum, usually as seedlings or young rosettes, rarely flowering, though two species seemed able to hold their own in competition with the parent form. The second method of search for the mutated individuals was also extensively employed. The following list gives the species observed in the field and those raised from seed collected there.

| PLANTS OBSERVED. | GROWN FROM SEED. |
|---|---|
| *O. lata.* 1889, 1894. | *O. lata.* 1887, 1889. |
| *O. nanella.* 1894. | *O. nanella.* 1889. |
| *O. spathulata.* 1886, 1804. | *O. lata-nanella*. 1889. |
| *O. elliptica.* 1886. | *O. rubrinervis.* 1889. |

Five of the new species originating in the garden were,

then, also found in nature. They occurred rarely, but usually several times in different years, and in such a manner that the later could not have been derived directly from the earlier individuals. These species are those which appeared most frequently in the experimental garden.

The first observation of a new form must not be regarded as its first appearance. Two of the new species, *O. elliptica* and *O. spathulata,* were found in the deserted potato field upon the first visit in 1886. It seems that the process of mutation was in full progress when the field was first visited. Whether mutation began when *O. Lamarckiana* began spreading over the deserted field or whether this characteristic was a much older one cannot be decided.

*Systematic Characteristics of the New Species.*

Discussions of questions of nomenclature are uninteresting enough for the scientist and will not be forced upon the general reader; but the source and nature of the material serving for any experiment or series of experiments is a matter of interest as well as of first importance, and before leaving the discussion of the origin of new species from *O. Lamarckiana* we must glance at the history of this species as far as it is known.

While it has shown itself quite constant under cultivation in Europe and America, it is not identical with any known member of the American flora, although it undoubtedly has its closest affinities with an American group. In the earlier European botanical writings, even so far back as 1635, there are references to a large-flowered Oenothera cultivated in European gardens, and this may have been the *O. Lamarckiana* as we now know it. De Vries and others have compared material of the species as we know it with the type material examined by Lamarck in the herbarium of the *Musée d'histoire naturelle.* Lamarck

saw neither living material nor specimens collected in the American habitat; his descriptions were prepared from dried specimens of plants cultivated in the garden of the museum. Two suggestions as to its possible origin seem most plausible; *O. Lamarckiana* may have been a species with limited distribution in "Virginia," as the region from which so many American plants were first taken to Europe was designated in the old herbals, and since then may have become extinct through the exploitation of the region by cultivation, or it may itself have originated by mutation from some other species in European gardens. Since that time, for over a hundred years, *O. Lamarckiana* has proved a constant type. And whatever may have been its origin, there can be no possible objection to its use as a subject for experimentation and one must express some surprise at the light way in which the results of these experiments carried on by De Vries and others have been cast aside as untrustworthy with the mere statement that *O. Lamarckiana* is only a garden variety or hybrid of some other form and that the new species are to be regarded as reversions to an ancestral type.

*O. Lamarckiana* is clearly differentiated from the other Oenotheras. The new species, too, are differentiated, not in one characteristic alone but in the assemblage of their characteristics.

### *Comparison of Old and New Species.*

It is particularly fortunate that Professor De Vries was able to carry out his experiments with a plant belonging to a genus having several other species which may serve for comparison, otherwise the objection would be urged that the characters exhibited by the new forms were not of specific value. And several species of *Oenothera* have been well known for a great number of years and recognized as distinct by systematists, so that objection from

that source is silenced, for the new forms not only differ as sharply and in many points from each other as do the old accepted species, but the individuals of a given new species are always identical in their characteristics, whether originating from *O. Lamarckiana*, from one of the new species, from crossing or from the offspring of self-fertilized parents of the same species and show no transitions either to other species or to the parent form.

Parallel cultivation of the recognized older species and the newly originated forms offers the best and only thoroughly satisfactory method of comparing their characteristics. De Vries was able to compare *O. muricata, O. biennis, O. suaveolens,* with two or three subspecies, *O. hirsutissima,* (*O. biennis hirsutissima* Torrey & Gray), *O. parviflora, O. cruciata* and a few others, while for other species his studies were limited to descriptions, figures and herbarium specimens. The result of these comparisons as stated by De Vries is that the known systematic species of the subgenus Onagra in the main do not differ otherwise than the group of forms originating from *O. Lamarckiana.* The groups are analogous.

*Transgressive Variability, Nutrition and Selection.*

In these comparisons of the characteristics or the assemblage of characteristics of the new species we must not ignore one of the strongest pillars of support of the selection theory, transgressive variability. The existence of transgressive variability has long been recognized by systematists. One has only to examine a number of individuals of two or more closely related species to find that some individuals seem to represent in some of their organs, at least, transitions between the two species.

The nature of the support which the existence of transgressive variability has been supposed to lend to the selection theory is very apparent, but its significance has doubt-

less been much overestimated. In the first place such transgressive variability is usually in respect to a single characteristic, or, if to more than one characteristic, all are not transgressive in the same way or to the same degree. Species, however, are commonly not limited by a single character but by a complex of characters. On the other hand, cultural experiments have demonstrated for a limited number of cases that seed from plants with the intermediate value does not produce plants with the measured characteristics in the same degree as the parent but those showing a strong reversion to the type of the species to which they may belong.

These general conceptions have been applied by De Vries to *Oenothera*. Two of the old and accepted species of Linnæus himself, *O. biennis* and *O. muricata,* were used for the first comparison. These differ conspicuously in the size of the flower. Measurements were made of flowers gathered without conscious selection from *O. biennis* and *O. muricata* individuals growing in the same locality. The mean length of calyx and corolla lobes for *O. biennis* was found to be 19-20 mm., while that for *O. muricata* was 14-15 mm., confirming the general impression of the difference between the two species. But the length of the calyx lobes in *O. muricata* ranged from 8-18 mm., while those from *O. biennis* exhibited a wider fluctuation of 14-33 mm. Thus the two species furnish a beautiful instance of transgressive variability, and indeed it would be quite possible to collect a series of flowers which would connect the smallest- with the largest-flowered form in an unbroken series of fluctuations. Further illustrations need not be given; they may be collected in unlimited number by anyone who chooses to take the trouble. The limits of species are transgressed but not obliterated by this fluctuating variability, which is in large measure dependent upon conditions of nutrition.

This transgressive variability is found among the new species. They show fluctuations which may be transgressive, but this is no evidence against their constancy. It is the permanence of the type which determines this.

Since we have instituted comparisons between the fluctuating variability of the old recognized species of the systematist and the newly originated species of the experimental garden, an examination of some of the experimental work on fluctuations is pertinent in this place.

What are the causes of fluctuating variations always present? It would greatly simplify matters if we might assume that the causes are purely internal, but unfortunately for the convenience of the systematist we have reason to believe that such is not the case.

Let us examine into this problem in a little greater detail. De Vries has devoted a special section in his large work to "Nutrition and Selection" and here we may point out the conclusions of the experiments performed with a view to determining the causes of fluctuating variability in the Oenotheras.

The length of the fruit in *Oenothera* is a variable characteristic, and the fruit of *O. Lamarckiana* at Hilversum was found in 1893 to fluctuate between 15 and 34 mm., with a mode, or greatest frequency, of 24 mm. The fruit lengths in this species are closely correlated with the vigor of the whole plant as indicated by the thickness of the stem, the longest and thickest fruits being found on plants with the largest stems.

An extensive series of experiments showed that when the plants were grown upon especially manured soil the fruit length was very greatly increased and that in fact a greater increase in respect to this character could be secured by appropriate conditions of nutrition than by the most careful selection. When the smallest fruited, and consequently the weakest, plants were selected as seed

bearers and the culture given the finest possible conditions for growth, the range of variation—the difference between the minimum and the maximum—was increased. In all these cases the curves of variation remained practically symmetrical.

Variability in the fruit-length of *Oenothera*, then, is largely dependent upon nutrition, and while it occurs in accordance with Quetelet's law of variation which has been shown to apply to the fluctuations of the measurable characteristics of so many animal and plant forms, it is also capable of experimental control. An increase or decrease in the value of a characteristic may be secured by special conditions, but the permanence of the effect is dependent upon the presence of these special conditions.

The general significance of these considerations should be apparent. Here in treating of the new species of *Oenothera* it is only necessary to call attention to the fact that these experiments show that transgressive variability cannot form an argument against the distinctness of the new forms.

### *Conclusions from the Several Families.*

We may now review the extensive sets of experiments in general terms and formulate the conclusions which they seem to justify.

New elementary species originate suddenly and without transition. This hypothesis has been advanced for garden varieties by various writers since the time of Darwin, but, as in almost all conclusions drawn from the field of practical horticulture, the data were open to serious question. But in the work of De Vries the conditions were quite different from those generally prevailing. The number of seed plants was relatively very small and they could be studied with the greatest care throughout their entire life history, so that there could be no doubt as to

their being typical *O. Lamarckiana.* Isolation of the plants during their first generations and their more certain protection in parchment bags with self-fertilization in the later generations made it certain that hybridization, unless in a very remote ancestor, had nothing to do with the results.

All of the hundreds of individuals belonging to the seven new species described above came from carefully studied and typical *O. Lamarckiana* ancestors, sometimes under observation for several generations. Their characteristics at a very early stage of the seedling and the classification of the young plants at that period led to no inconvenience when the individuals had assumed the more numerous and distinctive characteristics of maturity. In passing judgment upon some hundreds of plants, a few would be found of a doubtful position, especially such as had developed under conditions unfavorable to the normal development, but further growth showed these to belong undoubtedly to one of the groups into which the lot had been divided, or perhaps in rarer instances to represent a form now recognized for the first time.

Sometimes there were combinations of two sets of characters, as *O. lata nanella, O. scintillans elliptica.* Real transition forms between the new elementary forms or between these and the parent type did not occur.

That the new species are for the most part perfectly constant from the moment of their origin has been very strikingly demonstrated for several generations of various of the newly originated forms while not a single case of reversion to the parent type can be recorded. This showed itself true regardless of the number of individuals produced; for *O. gigas,* observed but three times, as well as for such frequently occurring forms as *O. albida, O, rubrinervis* and *O. nanella.* *O. lata* did not permit of a decision since it was always purely pistillate and could be propa-

gated only by crossing with some other species. The two forms which were found growing wild in the potato field, and which never again appeared in the culture, were as constant as the others when fertilized with their pollen, though *O. brevistylis* is almost sterile, producing a fruit with only occasional seeds.

The exception found in *O. scintillans* has been referred to already and its theoretical significance suggested. The evidence it offers is clearly very interesting but it does not speak strongly against the assertion of the constancy of the new forms. This constancy is a most important factor in the persistence of the newly originated species and a most striking and convincing illustration is that offered by the two new forms growing wild in the field at Hilversum. Here the struggle for existence is intense. The number of plants which may mature in its limited area is only a few thousands and the number of seeds supplied by a single individual would be almost sufficient for the area if all developed. But in spite of this, *O. brevistylis* and *O. laevifolia,* probably originating as did many of the new forms of the culture in at most only a few individuals, were able to hold their own for more than twelve years!

The third conclusion is that the most newly originated types represent exactly in their characteristics elementary species and not true varieties. To many people a variety is a form demonstrably originated from another. One of the most frequent objections to the theory of the origin of species by natural selection and one which has been most used has been that the origin of species has never been the subject of direct observation. As soon as a striking example was brought forward its rank as a species was immediately denied upon the ground that it was known to have originated from some other form and therefore could not be a species. It is evident that such quibbling should have no place in scientific literature. If a species

is a really definite unit it must be carefully limited and assigned its proper name wherever met and of whatever origin. In the general acceptance of the term varieties are distinguished by a single feature while species differ in almost all of their characteristics, in habit, as it may be called.

The most closely related elementary species differ in almost all their parts. To this the newly originated species of *Oenothera* form no exception. For this reason it has been impossible to give here a description of these forms. It has been said that to adequately describe and clearly differentiate the elementary species of a region would increase the size of the local floras five to tenfold. Often these differences are such as to show themselves only to the practised eye and then only in the plants as they grow in their native habitat, the characters of habit which there distinguish them so clearly being lost when specimens are taken for the herbarium. The new species of *Oenothera* show these numerous minor differences to a striking degree. Once carefully studied and described, there is no mistaking them at almost any period of their development, for these differences, though small, are sharp and distinctive. Nor do they depend upon mere habit of growth so that they are lost when material is prepared and preserved for future study and comparison in the herbarium. In this condition, when all plants lose many distinguishing characteristics, these new forms are still to be distinguished from each other and from the parent species with perfect ease; indeed with greater ease than *O. biennis* and *O. Lamarckiana,* two old and well established species of the systematist.

Only in *O. nanella* is there to be recognized a form which in accordance with general gardening terminology might be distinguished as a variety. It is also the only one for which comparable types may be found in the other

groups. Many species of the most widely separated systematic position have similar varieties in gardens. Red and white, proliferous and double, flowers, laciniate and smooth leaves, fasciated and twisted and pendulous, and smooth or unarmed stems are a few features which distinguish many constant garden forms as varieties rather than species, and everywhere in gardening literature one will see the Latin varietal names indicating these characteristics coupled with the most widely dissimilar species. The dwarf habit is one of these characters in point and a large number of garden plants with the varietal name *nana* or *nanella* are listed.

It is very interesting that this one form is the only one appearing in the Amsterdam garden which could legitimately be distinguished as a variety rather than a species. It was the hope of the experimenter that some real *varieties,* as for instance a white-flowered type, would appear in his beds, but this was never realized. While *O. nanella* may be considered a variety and in accordance with systematic usage be designated as *O. Lamarckiana nanella,* it must be remembered that so far as its behavior is concerned it is as good a species as the others. Indeed its constancy was subjected to even more severe test than the rest of the new forms. From an experimental point of view no sharp distinction is to be drawn between species and varieties.

The elementary species usually appear in a significant number of indiviuals at the same time or in the same general period of time. In the forms studied the number may be placed at 1 to 2 per cent. of the total number of individuals—an estimate which is rather too small than too large. This is a number which has been calculated sufficient to give a species well equipped for the struggle for existence a very good chance for establishing itself.

The new forms show no marked relation to individual

variability. *O. Lamarckiana* and all the newly originated forms show the usual fluctuating variability—the new forms sometimes in a greater degree than the parent—but there is no transition. The characters of the new forms are not dependent upon the differences attained by common variability. Cultured races may be secured by selection; they are not constant, however, but dependent upon selection for their perpetuity.

In the formation of new elementary species mutations occur without definite direction; the modifications embrace all organs and occur in almost every direction. The different organs may become larger or smaller, longer or shorter, broader or narrower, rougher or smoother, or the habit of growth may tend more to annual or more to biennial than that of the parent.

The question as to whether variations are haphazard or whether they occur in definite directions has not been without its polemic literature. The theory of Darwin and especially that of Wallace explained the origin of species by the selection of purposeless variations. The mutation theory explains the origin of the larger groups of forms, the Linnæan species, but not the elementary species, by the selection of the most fit elementary species. Just as according to the theory of natural selection, many individuals do not show the fortuitous variations which fit them exactly to their environmental conditions and are forced to the wall, so according to the theory of mutation only a few of the elementary species are adapted to meet the life to which plants are subjected and the most of them must perish.

The conditions observed in *Oenothera* under experiment offer most satisfactory evidence on this point, though the real fitness of the new forms can hardly be discussed until extensive experiments have been made. The two new forms found growing in the original locality were

able to hold their own for twelve years. Some of the new forms seem, in some respects at least, to be more vigorous than the parent type; others are so similar in vigor that no differences are to be distinguished, while many are evidently at a decided disadvantage in the weakness of their seedlings, their small size, their brittleness, their partial sterility or other characteristics. It was exceedingly difficult to bring some of the new forms to maturity, and these could certainly never persist in the keen competition in which plants must participate in nature.

The seventh and last conclusion must be drawn only very tentatively since, from the nature of the case, experimental evidence is difficult to obtain. That mutability appears periodically is indicated by the fact that the number of species found in a mutable condition is exceedingly small as compared with those in an immutable state. This may stand as a conclusion until further evidence may be obtained.

### C. VARIETIES IN NATURE UNDER CULTIVATION.

The degree to which the selection theory is dependent upon evidence afforded by the improvement of domestic varieties can hardly be overestimated. This has furnished almost the sole experimental basis for the promulgation of a theory otherwise resting upon comparative data. For the scientific world the theory of descent might have been generally established upon the data derived from paleontology, comparative anatomy and embryology, but the theory of natural selection could hardly have won recognition without the support derived from the attainments of breeders.

We have already discussed the soundness of these inductions in support of the theory of natural selection and have pointed out that there are very serious objections to the use of the evidence from horticultural selection which

restrict or almost nullify its significance for theoretical considerations. The words selection and improvement of the gardener's vocabulary are terms too vague to have much significance when transferred to scientific parlance. To the man of merely practical purposes, they may mean the isolation of a single desirable and constant minor species, "race," or "subspecies," from its congeners, the finding and preservation of a "single variation," the freeing of a constant race from the effects of crossing with its neighbors, the isolation of a mutation which has exhibited its latent presence by some slight external deviation, or finally, the terms may convey the meaning which is attributed to them in the generally accepted form of the selection theory, the accumulation of fluctuations. So long as the problem was the formulation of the broad outlines of the theory of descent it was not necessary to look into this evidence more critically, but we have reached the stage in which this can no longer be neglected.

The beautiful observations of Professor De Vries upon the evening primrose have shown that species differentiated in the totality of their characters may originate immediately from others. To some it may seem that the evidence afforded is so complete and satisfactory that recourse need not be had to the evidence offered by garden varieties. But an examination of trustworthy observations reveals the fact that when investigated in a systematic way, and with the precautions which should be a condition of all scientific experiment, garden varieties yield data of the highest value.

What are varieties? This query has been answered no more satisfactorily than the great question of systematists, "What are species?" The affirmation that varieties are incipient species has not cleared away the difficulties of the systematist, and in the absence of any generally

accepted code each has used his own pleasure in designating the forms he described as species or varieties.

Linnæus seems to have recognized two kinds of varieties, and the practice of many of the best systematists lends weight to this conception. There are the numerous constant and well-defined minor forms or subspecies, "the elements of the species," as De Candolle termed them, and there are the derived forms. In the first case a number of types are grouped together for the sake of convenience but with the tacit understanding that all are of equal rank and that no one can be considered as derived from another; there is no *forma typica* from which others may be supposed to have originated by minor modifications.

The second class of varieties differs essentially from the first. While their origin is generally involved in as much obscurity as that of the minor species, there is strong comparative and physiological and even historical evidence that they are derived from a known specific form. Varieties of this class are generally distinguished by a single characteristic although others are not infrequently, perhaps generally, associated with it.

The first point of evidence for their derivative nature is the frequency of their occurrence in widely different genera and families. Smooth varieties of hairy species, thornless varieties of armed species, white forms of red and blue flowered species are known to every one at all familiar with plants. These we may designate as true varieties; they differ from the typical species only in the stronger or weaker development of some special character or in its entire disappearance.

Varieties present certain advantages for investigation. Only a few members of our flora seem to be in a mutable condition in which new species are produced; the birth of a variety is probably a more common occurrence. Furthermore, according to quite generally accepted rules, a variety

is distinguished by a single characteristic and their study is largely the investigation of the nature and conduct of individual characteristics.

The mutation theory is not merely concerned with the observation of the origin of species or varieties and with the demonstration that there is an unmediated rather than a gradual process; it attempts to go farther and analyze the characters of species and reduce them to the component units or elements. Differing from their species in only a single character, varieties offer most favorable material for the study of the individual units.

*The Constancy of Varieties.*

It is quite generally assumed that varieties differ from species in their inconstancy and it behooves us first of all to look into the evidence upon which such an assumption is based.

Many "varieties" are only the parts of a single individual found as a "sport" by some horticulturist and propagated by cuttings or some other vegetative method. Such forms are often inconstant from seed and are in no small degree responsible for impressions of the inconstant nature of garden varieties. A similar source of confusion is hybrids propagated in a vegetative manner. The many thousands of plants are perfectly constant so long as they are only parts of the same vegetative body divided and grown separately, but when propagation by seed is attempted the variety is lost. Gardeners know full well the importance of these vegetatively propagated hybrids and some of the greatest successes of Luther Burbank and others are of just this kind. Another source of confusion is the improved races which are merely the accumulation of fluctuations by selection and so soon as selection ceases the betterment is lost and the "variety" reverts to the species.

Such ameliorated races or vegetative varieties are

often not to be distinguished from true and constant varieties by inspection, and their designation by the same term necessarily results in confusion and strengthens the impression of the inconstancy of "varieties" as compared with "species." The same is true of partial variability. Parts of the same individual grown on mountains may differ so widely from the part cultivated in the lowland as to deceive all but the one who knows the whole history; the experimental morphologist in his laboratory may cause the different parts of a single plant to assume strikingly different forms by controlling the conditions of light and moisture, but while these experiments bring serious misgivings as to the validity of many of the species catalogued in the floras they do not establish the inconstancy of species.

Accidental crossing is one of the greatest sources of error. The experiments which have been made upon this point need not be given space here, but the danger from this source cannot be too strongly emphasized.

Pollen may be carried by insects or wind for long distances and except with the greatest precautions one can not be confident that the packet of seed which he collects from his plants for his next year's crop has not a few which contain blood of another sort. In the case of varieties the danger is still greater. In the crossing of species the hybrid usually has a form intermediate between that of the two parent species, but seeds produced by fertilizing a variety with pollen from its species or *vice versa* produce plants which cannot be distinguished from the species. The character of the variety is there in a latent condition and it will make its appearance later.

The establishment of so many sources of error in the evidence for the inconstancy of varieties suggests that after all these forms may be constant. We cannot attempt to discuss the numerous cultural experiments which have

been performed by De Vries, Hildebrand, Hoffmann, Hofmeister, and others to test the constancy of varieties. When crossing with other types was prevented constancy was found almost without exception. Among thousands of seedlings of varieties differing in the characteristics of their floral structure or color, in smoothness or hairiness, in the armature of stems or fruits, in the forms of their leaves or the habit of the stem, no reversions to the parent form have been found. These experiments, and their number and extent is very great, evidence most forcibly against the assumed instability of these minor forms.

One of the most important proofs of the constancy of spontaneous or garden varieties is the great age of some of them. New forms are introduced every year, but it must be remembered that they are produced in a great number of ways and that their designation as varieties is merely a matter of convenience not always to be justified on scientific grounds. Many varieties were known to the Greeks and Romans, and when we come down to the more modern times of the herbals of the sixteenth and seventeenth centuries we find excellent illustrations of some which we have to-day.

### *The Origin of Garden Varieties.*

If, then, garden varieties are constant, what has been the mode of their origin? The evidence derived from the experiments with the evening primrose leads us to consider it most probable that their appearance has been by mutation, by sudden steps or bounds, and not by a gradual process of selection.

Historical records upon these questions are not very satisfactory, but a searching examination of such as exist tends to emphasize the probability of a sudden origin of the constant garden forms.

The instructive history of *Chelidonium majus lacinia-*

*tum* has already been mentioned. First observed in an apothecary garden in 1590 and never found in a wild state, it is to be assumed that this cut-leaved variety originated by mutation from the ordinary form and that it has been constant to this day. Of cut-leaved varieties among trees a long list might be given. Laciniate alders seems to have been produced by mutation at sundry times and cut-leaved maples are said to be produced quite frequently from seed of normal trees.

For many horticultural purposes, "weeping" varieties of trees are prized and a number of species have these varieties. They seem to have originated suddenly in single or at least very few individuals.

The smooth-fruited variety of the thorn-apple, *Datura,* originated suddenly and is of particular interest from the fact that it furnished the data for one of the earliest and clearest statements of the idea of mutation. Other cases of the origin of thornless varieties by mutation are well authenticated or highly probable.

The dwarf variety of *Tagetes signata* originated in a single individual among others of the normal form in Vilmorin's nursery in 1860. The dwarf Oenothera, *O. nanella,* may be recalled here and several other cases of the sudden appearance of constant dwarf varieties might be mentioned.

The remarkable origin of the cactus dahlia has already been described, and numerous other cases might be given were space available. As already stated, the accumulated evidence indicates for garden varieties a sudden rather than a gradual origin and justifies citing them as evidence in favor of the mutation theory. Sterile varieties are not easily explained on the ground of the selection theory, but they lend themselves most readily to the support of the mutation theory. Korschinsky has done a most important work in examining carefully into the history of garden

varieties for the purpose of determining the mode of origin of the various forms. His review is most comprehensive, covering the most diverse characteristics of stem and leaf and flower, and he concludes that the origin of new constant types has been by unmediated steps, by what we now term mutation, and not by the accumulation of fluctuations.

The history of some of these cases is most interesting, but these very general statements must suffice for the comparative data while we pass to the consideration of two sets of detailed and laborious experiments. The first is the origin of the "double" variety of the corn-flower and the second peloric form of the toad-flax.

*Origin of the Double Corn-Flower.*

Of all garden varieties perhaps the most common are the so-called double or filled flowers. Roses, hollyhocks, carnations and larkspurs are at once called to mind and the preparation of a complete list would be a serious task. This doubling usually consists in the transformation of stamens, and sometimes carpels as well, into petaloid structures.

Among composite plants, the sunflowers, daisies, marigolds, zinnias and others, we also meet with double varieties. Here the flowers are an aggregation of small flowers or florets. Of these, the outer row are frequently provided with large, conspicuous, strap-shaped or ligulate corollas and are designated as the ray flowers, while the others in the center of the disk have a short, tubular corolla, usually of relatively inconspicuous color as compared with the showy peripheral ones, and are known as disk or tubular flowers. Occasionally only tubular or "disk" flowers are present, as in Eupatorium and thistles, and again only ligulate flowers, as in the dandelion. Many forms originally with both disk and ray flowers have become "double"

by the transformation of the tubular corollas of many of the disk flowers into the ligulate corollas characteristic of the periphery. The most familiar examples of this are the Chrysanthemum, Zinnia and Dahlia.

With the hope of observing the production of a flower of this type from the normal form, De Vries cast about for a suitable species upon which to work, and finally chose the corn-marigold, *Chrysanthemum segetum*, which has a much prized garden variety *grandiflorum*.

Upon counting the ray flowers of the terminal heads of the plants grown from the seed which he secured from botanical gardens, indications of a mixture of the varieties were seen. The number of ray florets in the Compositæ is variable. This variability follows the law of Quetelet, and this variety•*grandiflorum* is distinguished by the possession of twenty-one ray flowers whereas the species has thirteen; around these numbers the fluctuations occur, the typical form sometimes bearing more than twenty-one rays and the *grandiflorum* type sometimes as few as thirteen.

The mixture was easily sorted into two constituent varieties by the selection of plants with thirteen- and twenty-one-rayed flowers. This process, however, requires much time since thirteen and twenty-one are only the typical worths around which the plants vary, and it is quite possible that a plant which is spared may be a widely fluctuating individual of the other type.

After three years' selection of twelve- and thirteen-rayed plants over 150 individuals were counted and found to have an average of exactly thirteen rays in the terminal head. The following year the same figures were obtained, so it was evident that the pure thirteen-rayed type had been isolated. The *grandiflorum* type was now isolated in the same way, the rays of the terminal heads of over

1500 plants being counted in the last year of the process of isolation.

In 1896 De Vries selected 500 plants from the 1500 with terminal heads with twenty-one rays and about the middle of August counted the rays of all the heads of the secondary branches as well. Among the many thousands of heads examined, all but two had twenty-one rays or less. This single exceptional plant was isolated and the heads allowed to be fertilized by pollen carried by insects from some others of the best plants of the group.

This slight deviation of structure in the secondary branches of this individual seemed indicative of some more profound change, for the number of rays could now be increased rapidly by selection. The progress was by veritable leaps. In the first year the average came up from 21 to 34, and then to 48 and 66 in the two succeeding generations.

These changes, however important, do not represent the real object of the experiment, which was to observe, if possible, the real origin of a double from a single form, —that is to say, a form in which some of the tubular flowers of the disk were transformed into ligulate or strap-shaped flowers similar to the rays.

Finally, in the fall of 1899, the fourth year of the selected race, the desired anomaly made its appearance in a single individual in which a few rays were found in the disks of three of the younger heads on one plant.

Two years' work eliminated the effect of crossing with other individuals and the double variety was quite as perfect as the other cultivated types of the same kind.

### *Origin of Peloric Toad-Flax.*

By peloria we understand the assumption of an actinomorphic or regular form by a normally zygomorphic or irregular flower. Presumably the prototypes of these ir-

regular flowers were themselves regular so that in a certain sense the assumption of the radially symmetrical form may be regarded as a reversion to a more primitive type.

This anomaly is described for a large number of forms, especially the two-lipped Labiatæ, Scrophulariaceæ and Gesneriaceæ. A discussion of the structure and manner of occurrence of these forms would be of great interest, but here we must limit ourselves to the most condensed treatment possible.

A gradual origin of such a deviation as peloria is not easily imagined. The phenomenon is seen very rarely or not at all in some genera or families while in others it may be observed with great frequency. Indeed examples of peloric races are not unknown. Seeds from such a one may be obtained for the foxglove and snap-dragon, *Digitalis* and *Antirrhinum*, which repeat the anomaly with great regularity though not always in all flowers or individuals. Another very constant example is the Gloxinia of our greenhouses. These showy plants have an erect, splendidly colored regular corolla while that of the prototype was more or less pendent and irregular.

Usually only a few of the flowers of any one plant are peloric, but in the toad-flax, *Linaria vulgaris*, all the flowers of a plant sometimes show this peculiarity. The corolla of *Linaria* is normally two-lipped and one-spurred, but in the peloric forms the two-lipped character disappears and the number of spurs is increased to five.

De Vries chose this species for experimentation because there was evidence that the wholly peloric variety had originated from the normal type with only occasionally a peloric flower in a number of instances and in widely separated localities. This renders it probable that it may appear again and under carefully controlled conditions of ancestry and environment. The object of the culture

was only to observe again what has presumably occurred in nature at various times.

The first recorded discovery of peloric toad-flax seems to be that of a student of Linnæus, whose find was described in 1744. Since that time it has been discovered in many places and under circumstances which render it most probable that it originated upon the spot from the normal type. In some cases the variety seems to have flourished for a time only to disappear later. The assumption of an independent origin of the peloric variety in each locality is supported by the fact that it is very difficult of fertilization by insects and ripe capsules with seeds have never been seen in nature, a fact which discredits at once the assumption of a possible common origin of the collections from the many widely separated localities.

In 1886 De Vries began a series of pedigree cultures of *Linaria* in the hope of being able to observe the origin of the peloric form. Roots of normal plants with one or two peloric flowers were transferred from a locality near Hilversum to his garden and flowered the following summer, producing seed for the second generation which was grown during the three following years. The plants flowered profusely, bearing in 1889 only one and in 1890 only two peloric flowers. Seed from the flowers of 1889 served for the continuation of the race, the third generation in 1890-91, which produced thousands of normal flowers but only a single five-spurred flower, which was pollinated by hand and produced ample seed for the culture of 1892. By sowing in the greenhouse and suitable methods of culture it was found possible to raise this and subsequent generations as annuals. Again only a single peloric flower was observed. The plant bearing this and one other individual were selected as seed parents—the toad-flax being quite sterile with its own pollen—and yielded an abundance of seed.

From this seed about fifty plants flowered in the autumn of 1894. Among these several peloric flowers were observed, eleven plants showing either one or two or even three of these abnormal flowers, but this cannot be regarded as remarkable since such individuals may occur in varying, though usually small, numbers in each generation. A single plant, however, was observed to produce only peloric flowers; the following year it bloomed again and confirmed the conclusions of the first year; the flowers were peloric without exception. Here, then, in a plant whose ancestry was definitely known to be of normal type for four generations, we have the first experimental mutation of a normal into a peloric race occurring suddenly and without transitions, only a single peloric flower having been found in the careful daily scrutiny of the thousands of flowers produced by the parents during two summers.

The ten cc. of seed from which the sowing for the fifty plants had been made was now nearly all sown and some 1750 flowering plants secured among which 16 wholly peloric individuals were found. The mutation occurs, therefore, in about 1 per cent. of the individuals. The possibility of crossing with the mutated individuals was excluded and the experiment continued. In subsequent generations the mutation was again repeated but with cultures limited in extent. In one case, however, two and in another one mutated individuals were obtained. These were related as "nieces" to those described above and appeared in the same manner, suddenly, completely formed and unaccompanied by transition to the normal form.

The external features of a plant must not serve as an ultimate criterion for the determination of its place in the system of classification. So far as may be seen by the eye alone it is often impossible to distinguish between an inconstant ameliorated race, a hybrid or an extreme

variation propagated by vegetative means, and a true species or variety. The true criterion of systematic worth is constancy in heredity and this is the test which must be applied to all mutations.

In the case of the toad-flax under consideration this is extremely difficult owing to the almost total sterility of the race cultivated. From over 1000 flowers carefully pollinated not a single normal fruit was secured but a rudimentary capsule yielded seed for 119 flowering plants of which about 90 per cent. were true to their type. Whether the ten per, cent. reversion was due to atavism or only to accidental crossing cannot be determined.

Summarizing these remarks on peloric forms we find that peloria, the assumption of a more or less regular form by a normally irregular flower, is not infrequently observed in nature, and in some families with much greater frequency than in others. In some cases it seems to be in a high degree heritable so that we may perhaps speak of peloric races. In other cases the phenomenon does not appear in every generation, but the latent potency which we may assume to be at the base of it becomes only occasionally active and we have what we may term iterative mutation. In the case of the toad-flax, De Vries has observed the origin by mutation of a perfectly formed peloric variety, *Linaria vulgaris peloria.*

### D. CONCLUDING REMARKS.

The conclusion which impresses itself upon the mind of the reader as he lays aside the first volume of Professor De Vries's work is that the origin of species has, in a few cases at least, become a matter of direct observation. This important process is no longer beyond the limit of actual observation and supported by only comparative data.

This is the point upon which the author himself lays the greatest emphasis and to a discussion of the method

of experimental evolution he devotes considerable space. For our present treatment it will be well to pass over these more special considerations and mention briefly the general conclusions derived from a comparison of the theories of selection and mutation.

No two individuals of a planting are exactly alike, expresses the variability—flowing, fluctuating, individual, statistical or whatever else it may be termed—of all living things. The selection theory postulates that these individual variations may be accumulated and fixed by selection. The mutation theory regards them as of no significance for the origin of species. Garden or local races may be developed or improved or acclimatization secured, but the limits of specific identity are not transgressed. The modifications accumulated by selection are not unlimited in extent and do not become independent of selection for their perpetuity. In sharp contrast to this betterment of forms by selection is the origin of new types. These appear suddenly, without transition from the parent type, and are constant from the first.

The statement that species have originated through natural selection in the struggle for existence requires some explanation before it may be embodied in the mutation theory. When the struggle for existence, or better the competition for existence, occurs between individuals of the same species, those least fitted to meet their life-conditions are forced to the wall and improved races or acclimatization results. This falls within the field of common variability. The competition may also occur between individuals of different species and then the *species* best adapted to the environment persists. But the struggle for existence and the survival of the fittest has nothing to do with the origin of the fittest. Before they may come into competition species as individuals must exist, and it is with special *species-forming* variability that the muta-

tion theory is concerned. The "survival of the fittest" has, then, two distinct meanings, the survival of the fittest individuals and the consequent development of local races or the securing of acclimatization in the constant specific type and the essentially different survival of the fittest species.

According to the mutation theory species have originated not by slow selection continued for hundreds or thousands of years, but by steps, through sudden though often very small transformations. Variations occur in plus or minus directions while mutations occur irregularly in all directions. Variations are of constant occurrence but mutations appear only from time to time.

The theoretical importance of the results of this long and laborious series of experiments carried out by Professor De Vries can hardly be overestimated. It is difficult for contemporaries to evaluate justly the interpretations which a naturalist assigns to the facts he has discovered and compiled. Many refuse to accept De Vries' positive iteration of the essential difference between fluctuating variability and mutation and the impossibility of accumulating the former by selection to the amount of fixed specific differences, but the results of the observations can hardly be discredited, and those who are acquainted with the literature of botany see everywhere series of other facts which seem to become clear and significant in the light of De Vries' discoveries and interpretations. It is not desired that these pages be a contribution to the too voluminous polemic literature of evolution, but that they shall furnish an epitome of the attempts and achievements of those who have been convinced of the discontinuity of variation with the consequent discontinuity of specific characters. It need only be remarked further that the researches of De Vries and others have built up a system of data which is impregnable to all but similar or improved

experimental methods. These investigations have raised the study of evolution from the morass of polemics, and in connection with the rediscovery and investigation of the Mendelian principles have given us the hope of the attainment of a real and definite knowledge of the organization of species.

Whatever be the present view of the generalizations which have been drawn, no one can deny the value of the method. Professor De Vries himself says: "Hauptsache ist, dass die Culturen im Garten uns verrathen, was in der freien Natur stattfindet, was sich dort aber der Beobachtung entzieht."

But while insisting on the fundamental value of the method, we must not lose sight of the intrinsic value of the materials assembled by De Vries in support of his theory. "The greatest contribution since that of Darwin," is the estimate of even those who are conservative in accepting the generalizations which De Vries has formulated. It is not given to one man to elaborate and promulgate alone an epoch-making doctrine, and several writers have perceived the importance of many of the conceptions which find their place in the comprehensive theory as it is now elaborated; but it is the fundamental importance of the results of long years of patient and successful experimentation which has won for Hugo De Vries the first place among those who have contributed to the renaissance of evolutionary studies.

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